RELATIONSHIP BETWEEN ROOT MORPHOLOGY AND NUTRIENT UPTAKE

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ABSTRACT

The exploitation of plant nutrients from soil and applied fertilizer by roots is dependent upon the morphology of the root system and the ability of different regions of roots to take up and translocate nutrients to the tops.

Although there is considerable information on the gross uptake and translocation of ions by plant roots, there are relatively few studies which specify the activities of various parts of roots.

We have used a technique in which roots are pulse labeled with radioactive phosphate, chloride, sulfate or zinc. The radioactivity along the roots is then measured by passing them through a recording radio chromatogram scanner. This technique has shown that lateral roots of the seminal root system of wheat seedlings, grown in soil for 14 days, account for over 70% of the uptake of sulfate and phosphate. Proportionally more phosphate is translocated from this lateral root zone to the tops than from the apical region of the roots.

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Soil temperature had a dramatic effect on root growth and morphology. Wheat roots grown at 10°C averaged 16 cm in length with 3-5 laterals compared with roots grown at 20°C which were 27-38 cm long with 57-82 lateral roots per main seminal root. Translocation of ^{32}P- phosphate to tops following pulse labelling was four times faster at 20°C than at 10°C.

The importance of lateral roots in the uptake and translocation of phosphate and the effect of soil temperature on root length and morphology raises the question of the possibility of breeding plants with specific types of root systems. If plant breeders can produce plants which have abundant lateral root production at realistic soil temperatures we should thereby obtain a much more efficient use of natural nutrients in the soil and also of applied fertilizer.

INTRODUCTION

The exploitation of plant nutrients from soil and applied fertilizer by roots is dependent upon the morphology of the root system and the ability of different regions of roots to take up and translocate nutrients to the tops.

Although there is considerable information on the gross uptake and translocation of ions by plant roots, there are relatively few studies which specify the activities of various parts of roots.

In our technique roots are pulse labelled with radioactive nutrients and the radioactivity along the roots measured by passing them through a recording radio-chromatogram scanner (Bowen and Rovira 1967, 1969; Rovira and Bowen 1968 a, b). This technique, with appropriate modifications, has enabled us to study the influences of environment and plant species on the patterns of uptake, loss, translocation and biochemical incorporation along roots (Bowen 1968, 1969, 1970; Rovira 1969). The results presented here deal mainly with wheat (*Triticum aestivum* L. var. Gabo) but essentially similar results occur with seedlings of *Pinus radiata*.

ROLE OF LATERAL ROOTS IN NUTRIENT UPTAKE

Wheat roots grown in soil at 20°C for two weeks were carefully removed, washed free of adhering soil and labelled for 15 minutes with radioactive phosphate, sulfate or chloride as described in Rovira and Bowen (1968 a). The roots were then washed for 5 minutes, mounted between cellulose tape and 4 cm wide Whatman No. 1 chromatography paper, dried at 50°C and passed through a radio-chromatogram scanner (Nuclear Chicago, Actigraph III). Previous experiments had established that radioactivity along the roots represents the sites of uptake as less than 10% of the phosphate, sulfate or chloride was translocated during the 15 minute uptake period, the 5 minute wash and the drying time (Bowen and Rovira, 1967).

This technique has shown that for the seminal root system of wheat seedlings grown in soil for 14 days, lateral roots accounted for 81% of the phosphate uptake, 79% of the sulfate uptake and 27% of the uptake of chloride. Figure 1 shows scans of the apical 25 cm of representative roots (40-45 cm long) which had taken up radioactive anions. Removal of lateral roots after the uptake and washing but before mounting on the paper, removed all of the uptake represented by the shaded parts of the charts.

By making use of the β emissions from ^{65}Zn we have used this technique to study the sites of uptake of

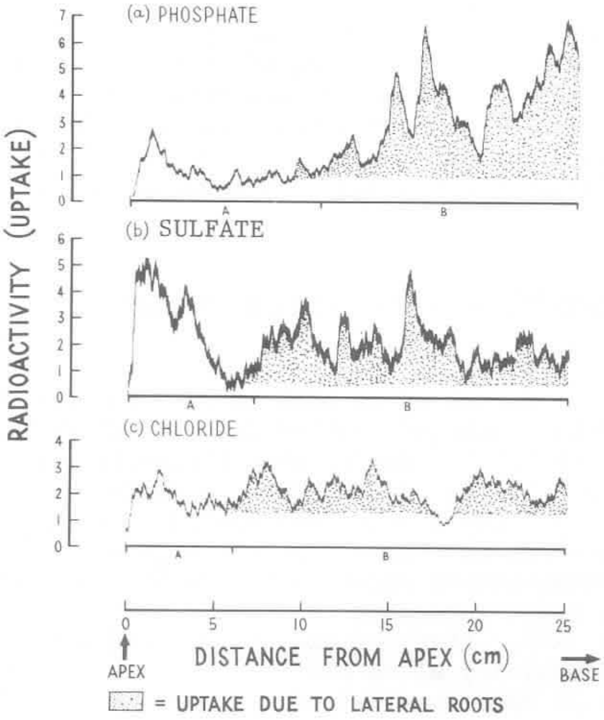

FIG. 1 Uptake of phosphate, sulfate and chloride by seminal roots of 14 day wheat grown in soil and labelled for 15 minutes in solution.

(a) Phosphate from solution of 5 × 10^{-4} M calcium sulfate + 5 × 10^{-6} M potassium dihydrogen phosphate with ^{32}P-phosphate at 400 μc/l.
(b) Sulfate from solution of 5 × 10^{-4} M calcium chloride + 5 × 10^{-6} M potassium sulfate with ^{35}S-sulfate at 800 μc/l.
(c) Chloride from solution of 5 × 10^{-4} M calcium sulfate + 2 × 10^{-3} M potassium chloride with ^{36}Cl-chloride at 200 μc/l.
A = Apical and prelateral zones
B = Root zone bearing lateral roots

zinc also into wheat, clover and pine roots; the uptake of zinc is greatly increased by the presence of lateral roots and the sites of zinc uptake in general corresponded with the sites of phosphate uptake (Rovira, Tiller and Bowen, unpubl.).

TRANSLOCATION OF PHOSPHATE FROM ROOTS

The results obtained by short term labelling revealed the tremendous increase in phosphate uptake following lateral root production. In order to assess the value of this uptake to the nutrition of the above ground parts of the plant it is necessary to measure the translocation of this phosphate from the different zones of the root. This was measured by labelling a large number of plants with ^{32}P-phosphate in 5×10^{-6} M potassium dihydrogen phosphate and 5×10^{-4} m calcium sulfate for 15 minutes, harvesting some immediately, transferring the remainder to non-radioactive potassium dihydrogen phosphate-calcium sulfate solution and after one hour, scanning roots and tops of these plants and calculating the decline in ^{32}P in various parts of the roots during this interval. We have shown that proportionally more phosphate was translocated from the lateral root zone than from the apical region (Fig. 2).

Russell and Sanderson (1967) in a study with older non-sterile barley roots using potometers, through which ^{32}P-phosphate was applied to small zones of roots, also found that the apex of the seminal primary root retained more phosphate than the zone behind the apex; however, they found proportionally less phosphate translocated from individual lateral roots than from the main axis and from nodal roots. These results with lateral roots are at a variance with our results - probably due in part to differences in experimental techniques, species and age of plant, and nutrition before and during the uptake experiments.

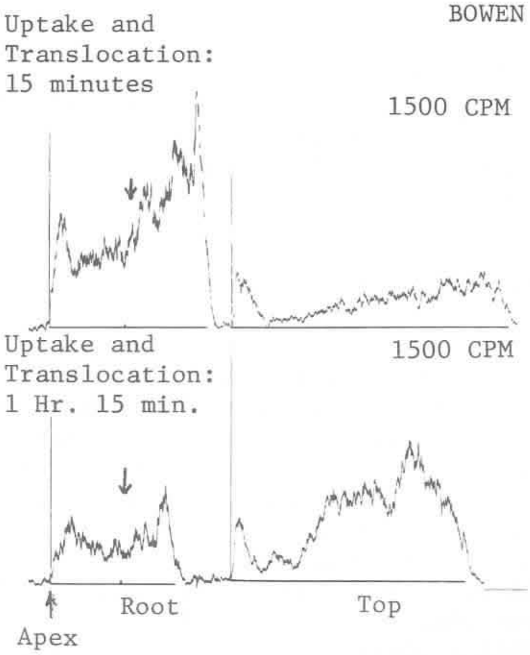

FIG.2 Translocation of phosphate from roots of wheat grown in nutrient solution for 5 days, pulse labelled with ^{32}P-phosphate for 15 minutes in 5 × 10^{-6} M potassium dihydrogen phosphate and 5 × 10^{-4} M calcium sulfate and then transferred to ^{31}P-phosphate for 1 hour. Only one of the three long roots of each wheat plant is shown for each scan. Roots and tops were scanned at 1500 cpm full scale deflection with 1.5 mm slit, ↓ Beginning of lateral root zone.

This technique was also used with wheat plants grown in soil at 20°C for 14 days; the seminal roots averaged 32 cm with 20 to 30 laterals per root and showed a high translocation of phosphate from the lateràl root zone after 1 hour 15 minutes.

EFFECT OF SOIL TEMPERATURE AND WATER ON ROOT GROWTH AND MORPHOLOGY

During some of the studies on the uptake of phosphate described above we observed that the patterns of uptake were affected by glasshouse conditions under which the plants were grown. This observation led to experiments in which plants were grown in a Red Brown Earth at root temperatures of 10°C and 20°C and uptake conducted at these temperatures.

Soil temperature exerted a marked effect upon the growth and morphology of wheat roots and Table 1 shows that the growth of the primary seminal roots and primary lateral roots of wheat is greatly reduced at 10°C. Thus, at low soil temperatures the growth of wheat may be limited by its inability to explore soil for less mobile nutrients such as phosphate.

TABLE I

Effect of Temperature and Water Content of Soil on (a) the Length (cm) of the Main Axis of Seminal Roots and (b) the Number of Lateral Roots/Axis of Wheat at 14 Days

Water Content of Soil (%)	Temperature of Soil (°C)			
	10		20	
	a	b	a	b
10	16	5	27	82
16	16	3	38	57

Soil water content affected root growth and morphology and hence the utilization of nutrients from both soil reserves and applied fertilizer by roots will be influenced by soil water content. Although the main axis of the primary seminal roots was reduced at the lower water content, the number and total length of primary lateral roots were increased; this resulted in a greater total length of root per plant. Another observation we made which has implications in the utilization of nutrients with low diffusivity through soil, e.g. phosphate, was that at 10 per cent water, root hairs were more abundant, longer and were not decomposed as rapidly as root hairs at 16 per cent water.

UPTAKE AND TRANSLOCATION OF PHOSPHATE AT 10°C and 20°C

Roots grown at 10°C showed a low uptake in the apical regions with an almost uniform uptake for the remainder of the root. By contrast, roots grown at 20°C with uptake at 20°C showed a high peak of uptake in the apical 3 cm, a low uptake behind the apex, and a very high uptake in the lateral root zone (Fig. 3). Bowen (1970) has found that roots of *Pinus radiata* showed patterns of uptake similar to wheat roots at low and high temperatures. These striking differences in patterns of uptake due to soil temperature indicate that our concepts of uptake along roots in models of soil-plant-nutrient systems must be adjusted to accommodate the influence of temperature.

Temperature affected translocation markedly, on raising the temperature of the uptake solution from 10°C to 20°C, with all tops at 20°C, translocation was trebled with roots grown at 10°C, and more than quadrupled from roots grown at 20°C.

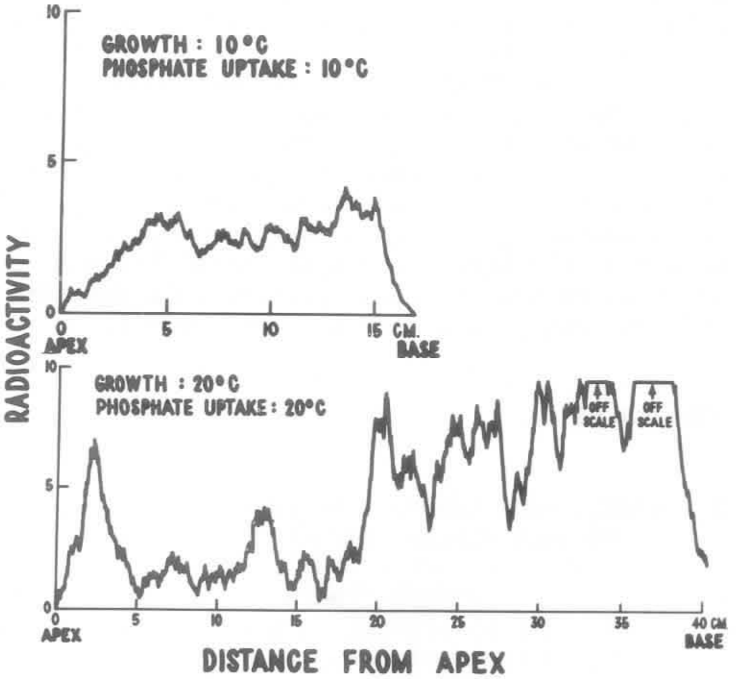

FIG. 3 Sites of phosphate uptake along wheat roots grown in soil at 10°C and 20°C with uptake from solution for 15 minutes at 10°C and 20°C respectively.

CONCLUSIONS

Integration of our results with the concepts of ion uptake from soil (Nye, 1966; Nye and Tinker, 1969) highlight the significance of lateral root production in (i) greatly increasing the total length of actively absorbing root which thus increases the volume of soil being exploited for nutrients, (ii) maintaining a high uptake rate and thus maintaining a high concentration gradient for diffusion of ions from soil to root over relatively large parts of the root and (iii) transporting a high proportion of absorbed phosphate to the tops. Unfortunately, little is known about the genetic and environmental factors affecting the initiation and growth of lateral roots. If we wish to improve the utilization of both fertilizer and soil phosphate by our domestic plants in southern Australia we should select and/or breed varieties which will grow faster and produce more lateral roots at soil temperatures of 10°C or less than do our present varieties.

REFERENCES

1. BOWEN, G.D. (1968) Chloride efflux along *Pinus radiata* roots. *Nature 218*: 686-687.

2. ________ (1969) The uptake of orthophosphate and its incorporation into organic phosphates along roots of *Pinus radiata*. *Aust. J. Biol. Sci. 22*: 1125-36.

3. ________ (1970) Effects of soil temperature on root growth and on phosphate uptake along *Pinus radiata* roots. *Aust. J. Soil Res. 8*: 31-42.

4. BOWEN, G.D. and ROVIRA, A.D. (1966) Microbial factor in short-term phosphate uptake studies with plant roots. *Nature 211*: 665-666.

5. ________________ (1967) Phosphate uptake along attached and excised wheat roots measured by an automatic scanning method. *Aust. J. Biol. Sci. 20*: 369-378.

6. BOWEN, G.D. and ROVIRA, A.D. (1969) New techniques to study nutrient relations in plants. *Atomic Energy in Australia 12*: 2-7..

7. NYE, P.N. (1966) The effect of the nutrient intensity and buffering power of a soil, and the absorbing power, size and root hairs of a root, on nutrient absorption by diffusion. *Plant Soil 25*: 81-105.

8. NYE, P.H. and TINKER, P.B. (1969) The concept of a root demand coefficient. *J. Appl. Ecol. 6*: 293-300.

9. ROVIRA, A.D. (1969) Diffusion of carbon compounds away from wheat roots. *Aust. J. Biol. Sci. 22*: 1287-90.

10. ROVIRA, A.D. and BOWEN, G.D. (1968 a) Anion uptake by plant roots: Distribution of anions and effects of micro-organisms. *9th Inter. Congr. Soil Sci. Trans. 2*: 209-217.

11. ____________________________ (1968 b) Anion uptake by the apical region of seminal wheat roots. *Nature 218*: 685-686.

12. RUSSELL, R.S. and SANDERSON, J. (1967) Nutrient uptake by different parts of the intact roots of plants. *J. Exp. Bot. 18*: 491-508.

Questions to Mr. Bowen

CLEMENTS: Did you restrict absorption to the very oldest part of some roots to determine whether they had adsorption there too in the roots, somewhat paralleling the work done at Duke with water?

BOWEN: The oldest roots we have used in studies reported here have been three week old pine roots and 14 days for wheat roots.

Previously I have taken mycorrhizal roots from established pine trees and found that in the older parts uptake was slow. Much of this appeared to be an adsorption phenomenon, which rather surprised me.

STEWARD: I have two questions, both quite brief. I gather that what you were plotting was absolute amounts of radioactivity along root. Have you put these on a concentration basis in the cells of the root?

The second point is: have you ever worked with a root that never branches, like narcissus?

BOWEN: Actual uptake is readily obtained from the accumulated radioactivity. We have not examined uptake on a per cell basis yet nor worked with plants whose roots do not branch. At present we are examining mechanisms of uptake along the roots, and some phosphate analyses of different parts of the root have been made.

POULSEN: I would like to ask how you would test your uptake. Is it on the basic dry weight of your root, or the fresh root weight?

BOWEN: With this technique it is difficult to obtain a fresh weight or a dry weight on parts of the root after scanning because you have mounted it.

We examine uptake per centimeter of root and, by measuring the radius of the root, we calculate this uptake per surface area; and it seems to me that this is the kind of thing that the plant is interested in.

POSSINGHAM: Have you ever done these experiments and then transferred the plants to water? How much of what you record is uptake in free space, and how much of it is incorporation?

BOWEN: We have examined the loss of phosphate from the root to calcium sulphate solution, and we find that in a period of three hours our loss of radioactive phosphate to the surrounding solution is between 3% and 5%, and from all portions of the above. We think, therefore, that any such loss does not distort our translocation data, which is obtained from "pulse chase" experiments.

What we measure is uptake and not exchange. Also uptake at 2°, or in the presence of potassium cyanide is eliminated. We examine biochemical incorporation by doing our initial scan, then extracting readily acid soluble inorganic phosphates by freezing and thawing in 0.1N perchloric acid which extracts all of these phosphates, but leaves the skeleton of the root.

We then scan the root, then remove nucleic acid fractions, rescan the same root and by differences, we can calculate incorporation into the readily acid-soluble phosphate, and the nucleic acid fraction and the residual phospholipid-phosphoprotein at each portion of the root.